

Diet composition and trophic niche of *Oedaleus asiaticus* (Orthoptera: Acrididae) in natural grasslands under different grazing pressure in Inner Mongolia, northern China

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Abstract: The n-alkanes in plant cuticular wax have been used as markers to estimate the diet composition and intake of grazing herbivores, but limited information is available about diet pattern of grasshoppers in natural grasslands based on the n-alkane technique. The objective of this research was to estimate the diet composition and trophic niche of *Oedaleus asiaticus*, a dominant grasshopper species, using the n-alkane technique in combination with quadrats. Experiments were conducted in three typical plant communities (*i. e.*, *Stipa klemenzi*, *Leymus chinensis*, and *Stipa grandis* communities) along precipitation gradients in the Inner Mongolian steppe from July to August of 2003. Twenty quadrats were selected randomly and clipped to ground level in each community to measure plant species diversity and aboveground biomass. Main plant species in each community and the feces of *O. asiaticus* were analyzed for concentration patterns of n-alkanes. Our results indicate that the diet composition of *O. asiaticus* in natural grasslands can be accurately estimated using the n-alkane technique, and it is significantly different under different grazing pressures and in different plant communities. The grasshopper shifted its diet pattern from a specialist (graminivorous) in *L. chinensis* and *S. grandis* communities to a generalist (mixed graminivorous) in *S. klemenzi* community. The overlapping indexes of trophic niche between *O. asiaticus* and sheep were 0.0619, 0.0172 and 0.1815 in *L. chinensis*, *S. grandis* and *S. klemenzi* community, respectively. The community structures of the vegetation (plant species diversity, biomass proportion, and frequency distribution) had significant influences on the diet composition of *O. asiaticus*. Grazing altered the plant community and indirectly affected the grasshoppers' food selection. The results suggest that certain competition may exist for food resources between grasshoppers and livestock.

Key words: *Oedaleus asiaticus*; plant community; grazing pressure; diet pattern; trophic niche; sheep; n-alkane technique; Inner Mongolian steppe

1 INTRODUCTION

Grasshoppers are important herbivores in the Inner Mongolian steppe of northern China, and *Oedaleus asiaticus* Bei-Bienko is the most dominant pest in the local region, especially in degraded grasslands, with outbreaks almost every year (Jiang *et al.*, 2003). An outbreak of *O. asiaticus* in 1999 affected almost 6 million hectares in the Inner Mongolian steppe. During that outbreak, the mean population density of *O. asiaticus* was up to 100

individuals /m². Wang (2004) observed that the population density was over 1 000 individuals /m² during an outbreak in 2002. Investigation of grasshoppers' food intake revealed that grasshoppers could consume 199.37 kg/ha of fresh forage annually when the population density was 11.2 individuals /m² and the forage consumed by grasshoppers was about 15% of aboveground plant biomass (Gandar, 1982; Feng *et al.*, 1995).

Study on the diet composition and food intake of grasshoppers can provide important information for protecting grasslands and maintaining plant

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diversity. Although many studies have been carried out to examine the diet composition of grasshoppers in the Inner Mongolian steppe by analyzing the contents of the grasshoppers' craws (Kang and Chen, 1994) and by directly observing the grasshoppers' food (Li *et al.*, 1983), conclusions of these studies were qualitative, recording only the plant species eaten by grasshoppers, but not quantitatively assessing the proportion of each plant species in the grasshoppers' diets.

With the development of grazing ecology, the technique of examining n-alkanes in plant cuticular wax described by Mayes *et al.* (1986) and Dove and Mayes (1991) has been used widely in studying grazing ruminants. However, this method has been mainly applied to livestock (Dove and Mayes, 1996; Berry *et al.*, 2000; Dove *et al.*, 2002; Ferreira *et al.*, 2004; Molina *et al.*, 2004; Smit *et al.*, 2005). Although little information is available on grasshoppers browsing on natural grasslands, the n-alkene technique could theoretically be used to estimate the diet composition of grasshoppers. Therefore, this study was conducted aiming: (1) to estimate the diet composition of grasshoppers using the n-alkane technique; (2) to quantify the diet of *O. asiaticus* in different plant communities; and (3) to analyze the effects of plant community structures on grasshoppers' food selectivity and trophic niche.

2 MATERIALS AND METHODS

2.1 Experimental sites

The study was conducted between July and August of 2003 in the Inner Mongolian steppe. Three types of plant communities, *i. e.*, *Stipa klemenzii*,

Leymus chinensis, and *Stipa grandis*, were selected along precipitation gradients from 200 to 350 mm (Table 1). For livestock grazing in large natural grasslands, the best grazing gradient is the distance from point sources of water (Pickup and Chewings, 1994; Teague, 2003). According to the degree and criterion of degraded grassland (Li, 1997), we used the distance between village and fenced grassland to calculate the appropriate grazing pressure for various types of livestock in this study (full use < 1.6 km; 50% use = 1.6 – 3.2 km; no use > 3.2 km or enclosure plot) (Holechek, 1988). Sheep and cattle grazed in natural grasslands in the day and camped in village of the region at night. In the *S. klemenzii* community, the 10-year fenced grasslands were selected as no grazing (NG), and moderate grazing (MG) and heavy grazing (HG) plots, which were arranged to 2 km and 1 km far away from the village, respectively (Liu *et al.*, 2013a). The same setup was used in the *L. chinensis* community, but the NG plot was fenced for 24 years. In the *S. grandis* community, the NG plot was fenced for 24 years, and the MG plot was selected outside the enclosure (Liu *et al.*, 2013b).

2.2 Sample collection

Main plant species and the feces of *O. asiaticus* and sheep, in each community, were sampled and the n-alkane concentrations in plant tissues were analyzed. Twenty quadrats (1.0 m × 1.0 m) of plants were selected randomly and all plants were clipped to ground level in each experimental plot to measure plant species diversity, aboveground biomass, and distribution frequency. Different plant species were separated by hand, dried at 65°C for 48 h, and then weighed. Each plant species, which had

Table 1 Main characteristics of three types of grassland communities in Inner Mongolia

Community type	Locality	Longitude and latitude	Annual precipitation (mm)	Altitude (m)	Grazing pressure	Density of grasshoppers (number of adults/200 nets)	Proportion of <i>Oedaleus asiaticus</i> (%)	Average height (cm)	Average coverage (%)
<i>Stipa klemenzii</i> community	Suniteyou Banner, Xilinguole League	N42°46'36", E112°40'25"	200	1 100	NG	15.3	70.6	19.3	33.0
					MG	32.6	95.3	16.6	17.5
					HG	24.8	95.5	14.0	27.5
<i>Leymus chinensis</i> community	Xilinhaote City, Xilinguole League	N43°32'59", E116°41'37"	350	1 260	NG	—	—	62.2	58.0
					MG	40.8	41.5	13.3	41.8
					HG	39.3	56.8	10.4	37.2
<i>Stipa grandis</i> community		N43°32'33", E116°33'18"	290	1 180	NG	14.5	40.1	55.6	53.3
					MG	53.3	70.5	11.9	28.0

NG: No grazing; MG: Moderate grazing; HG: Heavy grazing. The same below.

a proportion of dry matter (DM) that exceeded 0.5% of the total aboveground biomass for each community, was taken out, with more than 20 g as a subsample and ground through a 1-mm screen Wiley mill. Their n-alkane patterns were then analyzed.

The grasshopper species and densities were recorded randomly by sweep-net method in each experimental plot with 20 replicates in the morning (9:00 – 11:00). The 150 adults of *O. asiaticus* (male:female = 1:1) were kept in cages (1.0 m × 0.5 m × 0.5 m) and no food was added. The feces in each cage were collected 4 times after 6-hour intervals, dried at 65°C for 48 h, and analyzed for the n-alkane patterns.

2.3 n-Alkane analysis

2.3.1 Sample preparation: 1.0 g of all samples of herbage and feces were separately weighed, and placed into pyrex bottles with two replicates. Dual internal standards [0.2 mg n-docosane (C_{22}) + 0.2 mg tetratriacontane (C_{34})] and 10 mL ethanolic KOH of 1.5 mol/L were added to the samples. Pyrex bottles were sealed tightly and heated for 4.5 h at 90°C. The extraction was performed by adding 7 mL of heptane and 5 mL of distilled water, heating for 5 min at 60°C in the water container, shaking vigorously for 5 min, and then centrifuging at 2 000 r/min for 5 min to obtain a clear top layer. The upper solvent layer was transferred to a glass tube and the process was repeated to extract another 7 mL of heptane. Pooled extracts were evaporated with a compressed air stream from an air pump (Nisso μ -6000, made by Nisso Industry Co., Ltd.). The residues were then redissolved in 2 mL of heptane before applying them to the column containing 2 g Silica Gel 60 (230 – 400 mesh, Merck, Germany) with a 5 mL bed volume, and eluted with an extra 2, 2, and 4 mL of heptane, respectively. Thereafter, the eluate was evaporated to dryness using an air pump and redissolved in 1 mL of heptane, and then analysed for n-alkane concentration using a gas chromatograph (Mayes *et al.*, 1986; Dove, 1992).

2.3.2 Gas chromatography: For all samples, 1.0 μ L of the final and redissolved n-alkane solution was injected using an auto-sampler into a GC2010 gas chromatography (Shimadzu Company, Japan) fitted with a flame ionization detector. A TC-1 high resolution capillary column (0.25 mm in diameter, 30 m in length, and 0.25 μ m in film thickness) was used with a split auto-injection (split ratio 55:1). Flow rate for carrier gas (He) was 1.3 kg/cm² (about 1.0 mL/min) and 40 mL/min for N₂ and 0.5 kg/cm² (about 30 mL/min) for H₂. Column temperature was set at 200°C for 0.5 min initially, and then raised sequentially to 250°C at 20°C/min,

300°C at 10°C/min, 324°C at 6°C/min, 350°C at 3°C/min and down to 200°C in 3 min. The temperature for the injection and detector ports was maintained at 350°C.

2.3.3 Calibration of sample n-alkane concentration: A standard solution containing a mixture of odd and even n-alkanes from C_{20} to C_{36} was prepared with five different concentrations. The response factors for each n-alkane were calculated from peak areas and the known concentrations using a one-point or two-point calibration curve method. Extraction rate was calculated from two internal standards (C_{22} and C_{34}). The n-alkane concentrations in samples were calculated with reference to the difference in the extraction rates of two internal standards (Olivan and Osoro, 1999).

2.4 Data analysis

2.4.1 Estimation of diet composition: Diet composition of grasshoppers was determined using a least-squares optimization procedure (Salt *et al.*, 1994). This procedure was implemented using the n-alkanes analysis software EATWHAT (Dove and Moore, 1995). Optimal dietary proportion was obtained by comparing the concentrations of the n-alkanes from both fecal and vegetation samples within this procedure.

2.4.2 Diversity index and selectivity index: The Shannon diversity indexes of plants in the grassland community and in diets were calculated using the

formula: $H = - \sum_{i=1}^s P_i \times \lg P_i$, where H = plant diversity index, P_i = relative biomass of the species in the grassland community or diet (Zhang, 2004). The diet selectivity index was calculated using the formula: $SI = D/P$, where SI = index of selectivity, D = percentage of a species in diets, and P = percentage of the same species in the community (Wang *et al.*, 2001).

2.4.3 Trophic niche analysis: The niche breadth

was calculated using Shaanon-Wiener $B_j = - \sum_{i=1}^r P_{ij} \times \lg P_{ij}$, and the niche overlapping index was

analyzed using $O_{ik} = \sum_{j=1}^r \frac{P_{ij} \times P_{kj}}{C_j}$, where B_j is the niche breadth, O_{ik} is the niche overlapping index, P_{ij} is the proportion of herbivores i use of resource j , P_{kj} is the proportion of herbivores k use of resource j , and C_j is the relative abundance of the resource j in plant community (Zhang, 2004).

2.4.4 Statistical analysis: The SAS V6.12 was used for single factor analysis of variance ($P = 0.05$), and regression analysis. Two-factor analysis of variance was also used for the effect of grazing

pressure and season on the diversity of food and plant.

3 RESULTS

3.1 Plant community characteristics

3.1.1 Species and their biomass: The plant species composition and their dry matter proportion of aboveground biomass were different among different plant communities. Although there were 14 to 20 plant species in the *S. klemenzii* community, the aboveground biomass of 10 main species occupied more than 99% of the total aboveground biomass, and they were the main food resource of the grasshoppers (Table 2). The biomass of the dominant species *S. klemenzii* decreased with increased grazing pressure, while that of *Salsola*

collina increased and it became the most dominant species in the HG plot. In the *L. chinensis* community, there were 12 – 27 plant species, but the aboveground biomass of 7 main species occupied more than 99% of the total aboveground biomass. The biomass of the dominant species *L. chinensis* decreased with increasing grazing pressure, while that of *Potentilla acaulis* increased and it became the most dominant plant species in the HG plot (Table 2). There were 12 – 15 plant species in the *S. grandis* community, and the aboveground biomass of the 8 main species was more than 99% of the total aboveground biomass. In this community, *Cleistogenes squarrosa* replaced *S. grandis* as the most dominant plant species with increased grazing pressure (Table 2).

Table 2 Main plant species and their dry matter proportion (%) under different grazing pressures in three typical plant communities in Inner Mongolia

Plant species	<i>Stipa klemenzii</i> community			<i>Leymus chinensis</i> community			<i>Stipa grandis</i> community	
	NG	MG	HG	NG	MG	HG	NG	MG
<i>Achnatherum sibiricum</i>				14.88	2.49	0.03		
<i>Agropyron michnoi</i>				1.70	8.10	1.39	1.53	2.71
<i>Allium bidentatum</i>	0.87	3.46	1.01					
<i>Allium polyrhizum</i>	1.23	1.09	0.95					
<i>Anemarrhena asphodeleides</i>							8.66	0.13
<i>Artemisia frigida</i>	1.33	0.13	0.22					
<i>Cares duriuscula</i>	1.28	0.05	0.52					
<i>Carex korshinskyi</i>				5.95	6.81	6.66	8.44	2.19
<i>Cleistogenes songorica</i>	9.97	6.74	8.85					
<i>Cleistogenes squarrosa</i>				5.63	32.97	24.91	1.35	58.60
<i>Convolvulus ammannii</i>	1.46	0.61	1.40					
<i>Epheelra sinica</i>	0.11	0.12	2.63					
<i>Kochia pristata</i>	0.10	3.06	0.12				1.58	0.01
<i>Leymus chinensis</i>				32.19	18.79	6.11	23.44	13.37
<i>Potentilla acaulis</i>				0.06	0.01	42.42		
<i>Salsola collina</i>	20.22	75.28	81.65				5.36	10.19
<i>Stipa klemenzii</i>	62.88	9.09	2.14					
<i>Stipa krylovii</i>				36.01	30.49	18.23		
<i>Stipa grandis</i>							48.91	12.17
Total	99.45	99.63	99.49	96.42	99.66	99.75	99.27	99.37

3.1.2 n-Alkanes concentration of main plant species in three plant communities: Concentrations of odd alkanes were greater than adjacent even alkanes in each plant species, and the dominant alkanes were

C_{27} , C_{29} and C_{31} . The n-alkane patterns were different between plant species (Table 3), but the patterns were similar in the same plant species among the three plant communities.

Table 3 n-Alkane concentrations of main plant species in three plant communities (mg/kg DM) in Inner Mongolia

Species	C ₂₁	C ₂₃	C ₂₄	C ₂₅	C ₂₆	C ₂₇	C ₂₈	C ₂₉	C ₃₀	C ₃₁	C ₃₂	C ₃₃	C ₃₅
<i>Achnatherum sibiricum</i>	3	16	4	13	3	51	23	1 252	12	52	3	13	0
<i>Agropyron michnoi</i>	3	6	2	8	2	36	4	139	9	620	11	125	4
<i>Allium bidentatum</i>	2	8	2	16	2	92	22	331	20	233	16	24	0
<i>Allium polyrhizum</i>	3	112	17	106	17	239	22	693	65	4 177	57	94	3
<i>Anemarrhena asphodeleides</i>	2	45	9	73	11	157	18	357	27	380	13	18	2
<i>Artemisia frigida</i>	1	9	2	39	1	76	14	836	52	679	53	117	29
<i>Cares duriuscula</i>	4	6	3	7	2	21	6	274	31	303	23	58	2
<i>Carex korshinskyi</i>	3	4	2	5	3	28	8	491	29	848	14	75	3
<i>Cleistogenes songorica</i>	4	1	2	7	2	29	5	85	4	90	4	4	5
<i>Cleistogenes squarrosa</i>	5	7	1	8	3	42	6	159	8	265	8	92	5
<i>Convolvulus ammannii</i>	1	2	2	7	1	18	1	32	2	38	1	8	0
<i>Epheelra sinica</i>	1	5	2	10	1	25	5	236	7	48	10	7	0
<i>Kochia pristata</i>	1	3	3	41	4	116	15	559	24	335	19	71	9
<i>Leymus chinensis</i>	1	3	1	4	1	10	2	28	3	76	3	22	1
<i>Potentilla acaulis</i>	1	3	2	8	2	134	21	1159	18	355	6	36	8
<i>Salsola collina</i>	1	2	1	4	1	14	4	93	7	92	5	11	1
<i>Stipa klemenzi</i>	1	12	8	22	12	76	18	339	28	2 036	21	99	12
<i>Stipa krylovii</i>	2	15	3	22	6	171	12	474	21	2 521	33	1 892	88
<i>Stipa grandis</i>	5	5	2	10	3	49	6	321	22	2 014	20	153	14

3.2 Diet compositions of *O. asiaticus* in different plant communities

Although there were 10 main plant species in the *S. klemenzi* community, *O. asiaticus* mainly consumed 5 plant species under different grazing pressures (Fig. 1: A). *C. songorica*, *A. polyrhizum*, and *S. klemenzi* were preferred by grasshoppers, followed by *S. collina* and *A. bidentatum* (Fig. 2: A).

The diet composition of *O. asiaticus* was not obtained in the NG plot of the *L. chinensis* community because its vegetation cover and heights

were higher compared with those in the MG and HG plots (Table 1). Only three plant species were selected by *O. asiaticus* in the MG plot: *C. squarrosa*, *L. chinensis*, and *S. krylovii* (Fig. 1: B). However, 5 plant species were consumed in the HG plot. *L. chinensis* and *S. krylovii* were favorably selected by the grasshoppers, followed by *A. michnoi*, *C. squarrosa*, and *P. acaulis* (Fig. 2: B).

Four plant species were selected by *O. asiaticus* in the *S. grandis* community in the following order of preference: *L. chinensis*, *C. squarrosa*, *S. collina*, and *S. grandis* (Fig. 1: C; Fig. 2: C).

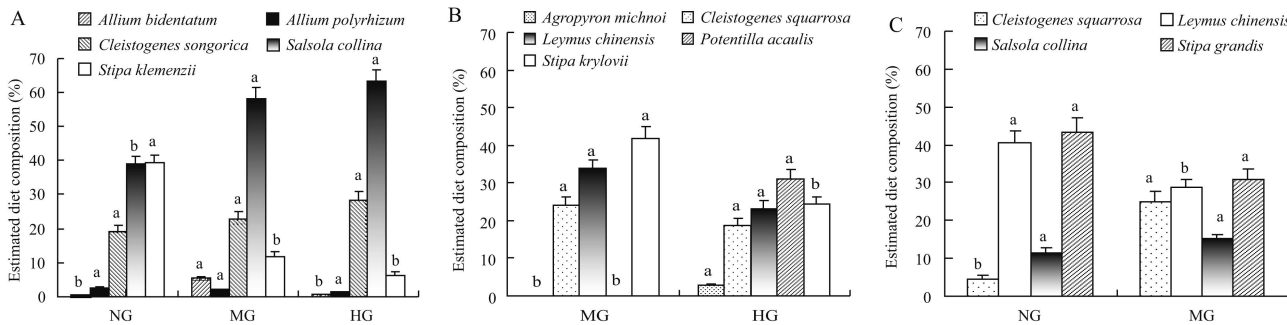


Fig. 1 Estimated diet composition of *Oedaleus asiaticus* using n-alkane technique under different grazing pressures in three types of plant communities in Inner Mongolia

A: *Stipa klemenzi* community; B: *Leymus chinensis* community; C: *Stipa grandis* community. The same for Figs. 2 and 3. Data in the figure are mean $\pm$ SE. Different letters above bars of the same plant species under different grazing pressure indicate significant differences ($P < 0.05$).

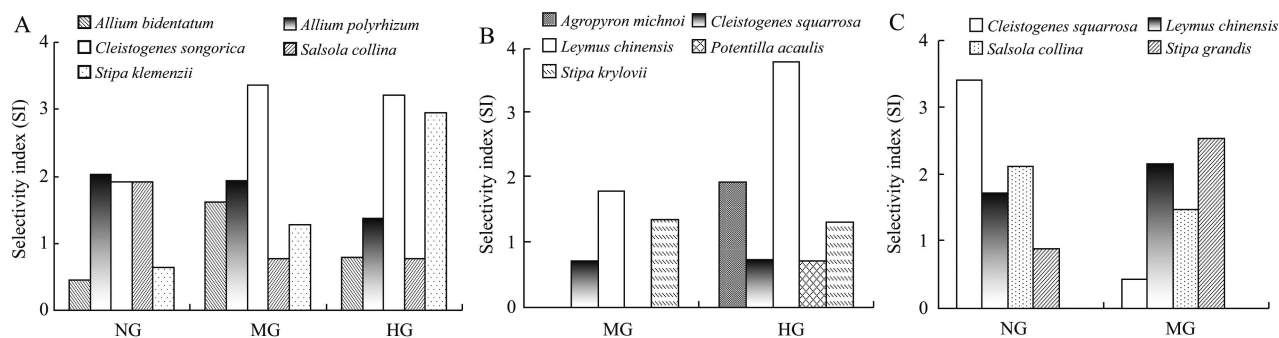


Fig. 2 Selectivity index (SI) of the plant species in three types of plant communities in Inner Mongolia

3.3 Relationship between selectivity index (SI) and grazing pressure

An SI value greater than 1.0 indicates that the plant species is preferred by the grasshoppers. We found that the main food resources of grasshoppers were grasses and forbs in the three communities examined (Fig. 2). The grasshoppers' preference for *A. polyrhizum* and *S. collina* decreased, while their preference for *C. songorica* and *S. klemenzii* increased with increasing grazing pressure in the *S. klemenzii* community. The grasshoppers' preference for *A. bidentatum* was the highest in the MG plot (Fig. 2; A). In the *L. chinensis* community, the preferred plant species were *L. chinensis* and *S. krylovii*. When the food resources were poor, the grasshoppers preferred *A. michnoi* and *P. acaulis* in the HG plot (Fig. 2; B). In the *S. grandis* community, the grasshoppers' preference for *L. chinensis* and *S. grandis* was greater in the NG plot

than in the MG plot, the opposite result was observed in the *C. squarrosa* and *S. collina* communities (Fig. 2; C). These results indicate that *O. asiaticus* preference is altered by food resource availability due to different grazing pressure in the three communities.

3.4 Relationship between diet composition and plant community characteristics

The plant diversity index (PDI) decreased with increased grazing pressure in the three plant communities (Fig. 3), but the dietary diversity index (DDI) increased in the *L. chinensis* (Fig. 3; A) and *S. grandis* communities (Fig. 3; C) and decreased in the *S. klemenzii* community (Fig. 3; B). The DDI was greater than the PDI in the MG and HG plots for the *S. klemenzii* community but lower in the MG plot for the *L. chinensis* community and in the NG plot for the *S. grandis* community (Fig. 3).

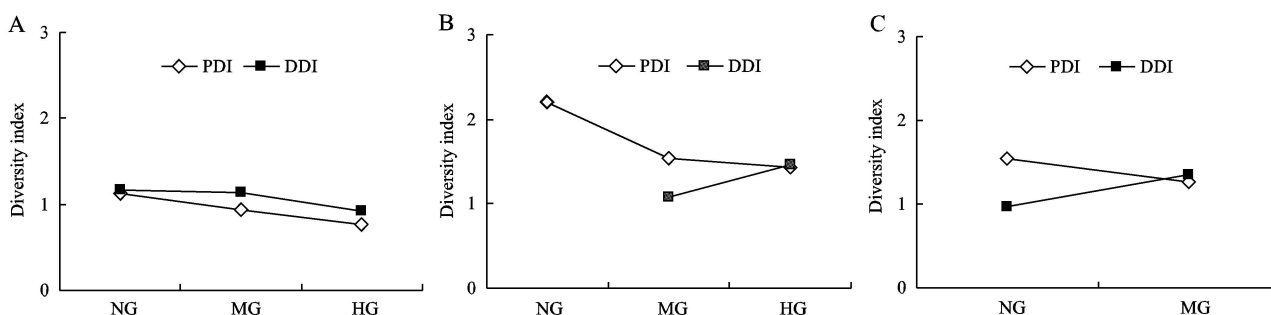


Fig. 3 Relationship between the dietary diversity index (DDI) and the plant diversity index (PDI) under different grazing pressures in three plant communities in Inner Mongolia

3.5 Trophic niche breadth and overlap between two herbivores *O. asiaticus* and sheep under different grazing pressures in different communities

3.5.1 Trophic niche breadth: Trophic niche breadth between two herbivores *O. asiaticus* and sheep was not the same under different grazing pressures in different communities (Table 4). Under the moderate grazing pressure, the breadth of sheep niche was the widest in *S. grandis* community. However, the breadth of sheep niche was narrowed

with increasing grazing pressure in the *S. klemenzii* community and the *L. chinensis* community. This result was due to the fact that sheep do not have the opportunity to do selective feeding as the available herbage become lower with increasing grazing pressures. However, in *S. grandis* community and *L. chinensis* community, the trophic niche breadth of *O. asiaticus* was increased with increase of grazing pressure, indicating that the forage species which *O. asiaticus* preferred are abundant with increasing

grazing pressure. However, in the *S. klemenzi* community, the trophic niche breadth of *O. asiaticus* was being narrowed with increase of grazing pressure, suggesting that the food resources become scarce with the decrease of forage species and grassland being severely degraded under heavy grazing.

3.5.2 Trophic niche overlap: The degree of trophic niche overlap reflects the degree of similarity of resource usage and the potential competition between species. In *S. klemenzi* community, the

degree of the trophic niche overlap between the two herbivores was the highest (Table 5). This indicated that the food was scarce, available resources were limited, and strong competition for resource existed between the two herbivores in this community. However, in the typical steppe communities, especially in *S. grandis* community, the degree of the niche overlap was lower between the two herbivores. This result indicated that food was abundant, and the food resource competition between herbivores was weaker in these two communities.

Table 4 Coefficient of trophic niche breadth of two herbivores under different grazing pressures in three communities in Inner Mongolia

Plant community	<i>Stipa klemenzi</i> community			<i>Leymus chinensis</i> community			<i>Stipa grandis</i> community	
	NG	MG	HG	NG	MG	HG	NG	MG
Sheep	–	1.27	0.92	–	1.31	1.19	–	1.43
<i>Oedaleus asiaticus</i>	1.17	1.15	0.92	–	1.07	1.45	1.12	1.36

Table 5 Overlap of trophic niche both sheep and *Oedaleus asiaticus* in three plant communities

Herbivores	<i>Stipa klemenzi</i> community		<i>Leymus chinensis</i> community		<i>Stipa grandis</i> community	
	Sheep	<i>O. asiaticus</i>	Sheep	<i>O. asiaticus</i>	Sheep	<i>O. asiaticus</i>
Sheep	+	0.1815	+	0.0619	+	0.0172
<i>Oedaleus asiaticus</i>		+		+		+

4 DISCUSSION AND CONCLUSION

4.1 The methods of estimating diet composition of grasshoppers

Many methods have been used to estimate the diet composition of grasshoppers, but these methods can only classify which forage species are eaten by grasshoppers through direct observation of grasshoppers eating behavior in cage experiments (Gangwere, 1961; Li *et al.*, 1983), morphologic analysis of the grasshoppers' alimentary tracts (Tyrcus, 1971), or analysis of grasshopper feces (Gangwere *et al.*, 1998). These methods are complex and labor intensive, and require longer experimental periods. Moreover, microscopic examination of craw contents (Kang and Chen, 1994) requires researchers to identify the microstructure of each plant, which in turn requires considerable training to ensure that researchers make accurate estimations of the grasshoppers' diet composition. Previous studies have shown that with highly trained operators, even a variable proportion of the plant fragment remains unidentifiable (Holechek *et al.*, 1982; Norbury and Sanson, 1992). Because n-alkanes in plant cuticular wax were not digested by herbivores (Dove and Mayes,

1991), theoretically, the diet composition of grasshoppers could be estimated by comparing the concentration of n-alkanes in herbage with that in grasshopper feces. In this technique, fecal recovery rates of n-alkanes are key values in estimating diet composition of grasshoppers (Dove, 1992), and they have been measured by the same author in 2007 in natural grasslands, but the data are not published at present.

4.2 The diet composition of *O. asiaticus* and its affecting factors

Kang and Chen (1994) reported that 11 grasshopper species in *L. chinensis* and *S. grandis* communities could be divided into 5 groups in trophic niches by microscopic examination of craw contents. *O. asiaticus* was considered a graminivorous species, which consumed 12 plant species. In our study, *O. asiaticus* consumed 7 plant species, and mainly selected grasses, such as *L. chinensis*, *C. squarrosa*, *S. grandis*, and *S. krylovii*, in both communities. However, in our study, *O. asiaticus* preferred grasses (*C. songorica* and *S. klemenzi*) and forbs (*S. collina*) (Fig. 1), and became a mixed graminivorous species in the *S. klemenzi* community (He and Zheng, 1997). These results further indicate that the diet composition of grasshoppers could be estimated using the n-alkane

technique. The alkane marker technique was a better method for estimating the diet composition of herbivores (Dove and Mayes, 1991), because the method was a chemical approach, and therefore more accurate, and simpler and quicker for researchers to apply. Each plant species and the proportion of each plant species that was eaten by herbivores could be distinguished quantitatively.

There are many factors affecting the diet composition of grasshoppers, including climate, drought, high temperature (Evans, 1992), vegetation types, plant coverage, and grassland degenerative degree (Qiu and Li, 1997). Our results revealed that the diet composition of *O. asiaticus* varied with food resources under different grazing pressures and in different plant communities. When herbage resources (aboveground biomass) are abundant and plant species are diverse in the community, grasshoppers can select freely from preferred forage species, whereas grasshoppers may be forced to select previously undesirable plants if food resources are shortage (He and Zheng 1997), such as in the HG plot of *L. chinensis* and *S. klemenzii* communities in our study. Favorable plant species and their proportions decreased with increased grazing pressures (Wang, 2000). This change led to decreased PDI with increased grazing pressures in three communities. As *O. asiaticus* showed a great preference for food resources (Kang and Chen, 1994), the DDI was higher than PDI (Fig. 3), and the SI was higher in the HG plots than in MG or NG plots in the *S. klemenzii* community (Fig. 2). Similar trends were found in the *L. chinensis* and *S. grandis* communities. These results showed that the DDI of *O. asiaticus* increased with increased grazing pressures and the diet composition of *O. asiaticus* changed with a change in plant community. Grazing indirectly affected the food selectivity of grasshoppers.

4.3 Trophic niche of *O. asiaticus*

The niche breadth is the sum of different resources of a population using in a plant community (Zhang, 2004). Generally speaking, when the food is abundant, herbivores tend to gain those more achievable food resources by the most suitable and convenient way which makes their niche narrowing. In comparison, when the food is lack, herbivores will expand their potential of using more resources which makes their niche widening (Wang, 1996). The food resource for sheep reduced significantly with increasing grazing pressure in *S. klemenzii* community, and *S. collina* became a main food source for sheep in our study (Table 2), which

resulted in a single diet composition and a narrowed trophic niche for sheep. This result is due to a unique food source and no selectiveness for grazing sheep in the community. The *S. collina* is a product of seriously degraded grassland (Zuo *et al.*, 2006), therefore, it is inevitable to narrow sheep trophic niche when the food resource is at a state of serious shortage. This finding is consistent with the above general conclusions (Wang *et al.* 1996; Zhang, 2004). Our experiment also verified the fact that seriously degraded grassland is not suitable for grazing (Wu and Yang, 1994). With increasing grazing pressures in *L. chinensis* and *S. grandis* communities, the amount of *L. chinensis* and *S. grandis* decreased (Han *et al.*, 1999), which forced *O. asiaticus* to expand its food ranges, and further widened its trophic niche. Because the plant composition of grassland was changed with grazing (Wang, 2000, 2001), the preference of *O. asiaticus* to plant species increased in *S. klemenzii* community with increasing grazing pressure (Kang and Chen, 1994), which resulted in a narrowed trophic niche. The changes of niche breadth for some grazing animals in different communities show that food range is limited by food resource. When the food resource is abundant, the grazing animal has an opportunity to do selective feeding, which results in a narrowed trophic niche. When there is a shortage of available food, the selective feeding of grazing animal decreases, which results in a widened trophic niche. However, extreme limitation of food resource can narrow the trophic niche because herbivores have no way to select food under this circumstance.

The existence of niche overlap among different communities means the existence of competition for food resource, particularly when the food resource is scarce (Baldi *et al.*, 2004; Zielinski and Duncan, 2004). In our study, the niche breadth of *O. asiaticus* was close to that of sheep in three communities, and the higher overlap was found in *S. klemenzii* community, showing that they have similar recipe and compete with each other for available food resources in these communities, particularly in degraded *S. klemenzii* community. There are a number of factors that lead to niche overlap of herbivores. Selective feeding and availability of food resources are the two main factors (Wissinger, 1992; Wang *et al.*, 1996). In our study, the trophic niche breadth of the *O. asiaticus* is broadened with increasing grazing pressure in the two typical grassland communities. This is due to the fact that available food resources decrease with increasing grazing pressure, which results in its food

composition diversification. But in degraded *S. klemenzii* community, the trophic niche breadth of *O. asiaticus* was narrowed with increasing grazing pressure, mainly due to the fact that the diversification of food resource reduced and the plant species that *O. asiaticus* preferred increased. This implies that grazing is a direct cause of degraded grassland in *S. klemenzii* community, and the plant species that *O. asiaticus* preferred increased in the degraded grassland (Liu *et al.*, 2013a). Consequently, the plant species that grasshopper prefer to eat increase, which result in the outbreak of grassland rodent pests. Once the rodent pests outbreak, they can threaten the food resources of sheep and thus affect sheep population and performance. Therefore, controlling grazing pressure and rational use of grasslands are the most effective ways to prevent the outbreak of grassland rodent pests. In addition, controlling the population of pest density and preventing pest occurrence are of a great practical significance in protecting grazing animal food security.

4.4 Conclusion

Our study indicates that the n-alkane technique can be used to assay and ascertain the diet composition of wild herbivores in natural grasslands, and grasshoppers can change their diet patterns in different communities. There is strong competition for food resources between grasshoppers and livestock. When grasshoppers overrun grasslands, the food resources of livestock are threatened, so it is necessary to prevent grasshopper outbreaks in natural grasslands.

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内蒙古天然草原不同放牧压力下亚洲小车蝗的食性及营养生态位

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摘要: 植物表皮蜡质中的饱和链烷作为内源指示剂广泛用于评价放牧家畜的食性和食量, 但用于天然草原蝗虫食性的评价研究较少。为了探讨天然草原蝗虫的食性及其生态位变化, 本研究以内蒙古天然草原为研究对象, 于 2003 年 7-8 月沿降水梯度选择 3 种典型植物群落(小针茅 *Stipa klemenzii*、羊草 *Leymus chinensis* 和大针茅 *Stipa grandis* 群落), 在每个植物群落不同放牧压力下小区随机做 20 个植被样方, 样方内植物齐地面刈割, 测定其地上生物量和物种多样性, 取主要植物种测定其链烷模式, 同时采集放牧小区优势蝗虫种亚洲小车蝗 *Oedaleus asiaticus* 的粪便, 测定其链烷模式, 运用链烷技术评价蝗虫的食性及其营养生态位。结果表明: 不同植物群落中优势牧草种类及其比例不同, 其链烷模式存在种间差异, 链烷技术可以评价亚洲小车蝗的食性。亚洲小车蝗的食性在不同植物群落及不同放牧压力下存在显著的差异, 在羊草和大针茅群落中, 亚洲小车蝗是禾草采食者, 主要采食羊草和糙隐子草 *Cleistogenes squarrosa*, 且与绵羊的营养生态位重叠指数较低, 分别为 0.0619 和 0.0172; 在小针茅群落中亚洲小车蝗是杂类草采食者, 主要采食无芒隐子草 *Cleistogenes songorica*、猪毛菜 *Salsola collina* 和小针茅, 且与绵羊的营养生态位重叠指数较高, 达到 0.1815。因此, 放牧不仅改变了群落的植物种类组成, 而且直接影响了亚洲小车蝗的食物组成, 二者对食物资源利用存在一定程度的竞争。

关键词: 亚洲小车蝗; 植物群落; 放牧压力; 食性; 营养生态位; 绵羊; 链烷技术; 内蒙古典型草原

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